

THE COMPARATIVE MORPHOLOGY OF THE WINTERACEAE VI. VASCULAR ANATOMY OF THE FLOWERING SHOOT

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With four plates and one text-figure

Two previous papers (Bailey and Nast, 2, 3) of this series have dealt with the vascular anatomy of the stamens and carpels of the Winteraceae. In order to complete a floral anatomical study of the family, the present paper will be devoted to an examination of the pedicellar and toral vascular systems and to a discussion of certain implications arising from that examination.

MATERIAL AND METHODS

Herbarium material of twenty-six species of *Drimys*, *Bubbia*, *Pseudowintera*, and *Belliolum* was available for dissection and sectioning. *Zygo-gynum* and *Exospermum* are not included because no adequate floral specimens were obtainable. Although serial sections were indispensable for tracing the details of the intricate vascular system, flowers cleared in a weak solution of NaOH (Bailey and Nast, 2) were helpful in observing the general vascular pattern and for checking with the sectioned specimens. All material was first heated in water and then treated in NaOH before embedding in paraffin. The NaOH not only restores the specimens most nearly to their original size and shape, but also frees the cells from extraneous substances, which interfere with the clarity of the vascular strands. The usual alcohol-xylene-paraffin embedding method was followed. Slides were stained with Haidenhain's haematoxylin and safranin and mounted in clarite.

The vascular cylinder was drawn as if opened and flattened out in *figures 7, 9, and 12*, and the vascular strands were depicted to show as nearly as possible their approximate size and the size of the interfascicular regions. Some slight distortions occur in order to make room for appendage traces. Small traces are somewhat enlarged for clarity in reproduction. In *figure 11* the toral bundles are represented by xylem and phloem, and the traces by xylem only.

TERMINOLOGY

It will be necessary, before beginning a description of the floral anatomy, to discuss the terminology used in this article. There has been great confusion and looseness in the use of stelar nomenclature. It seems desirable, therefore, to refer to the original use of stelar types to determine the most appropriate term for the many-bundled angiospermic stele. In 1899 Jeffrey (7) used *siphonostele* as referring to a tubular vascular axis in contrast to protostele. He subdivided the siphonostele into *phyllosiphonic* stele, one with foliar gaps, and *cladosiphonic* stele, one with ramular or branch gaps

and no foliar gaps. The siphonostele may be either *ectophloic* or *amphiphloic* (8). When the siphonostelic central cylinder “. . . ceases to be obviously tubular . . .” he referred to it as *adelosiphonic* (9). In 1901 Gwynne-Vaughan (6) defined the term *solenostele* as “. . . a single hollow cylinder with phloem and phloeterma on either side, the complex continuity of which is interrupted only by the departure of the leaf-traces; the gaps thus produced being closed up in the internode above before the departure of the next leaf-trace.” He further stated that “According to Jeffrey’s terminology, solenostely would be regarded as a special type of *amphiphloic phyllosiphony*.” Thus the tendency to consider solenostele and siphonostele as synonymous is erroneous if original definitions are to be considered. In 1902, Brebner (4) used the term solenostele according to Gwynne-Vaughan’s definition and coined the new term *dictyostele*, “A vascular tube with large ‘overlapping’ leaf-gaps, so that the whole structure becomes a network of vascular strands or meristeles. The meristeles are concentric.” He further defined dictyostele “. . . as *siphonic* when the network is simple or tubular and *adelosiphonic* when complex, i. e., ceasing to be obviously tubular.” The erroneous use of dictyostele in anatomical articles and in textbooks as a term for a dissected siphonostele with either collateral or bicollateral bundles is unfortunate, since Brebner was very definite in stating that the bundles of a dictyostele are *concentric*. Furthermore he applied dictyostele to a special type of *fern* stele, and used the term *eustele* for vascular cylinders such as are present in most angiosperms. His definition, “It (eustele) consists of a ring of collateral or bicollateral meristeles, and includes the pericyclic and medullary ground tissue,” very clearly refers to the “dissected” angiospermic type of stele. The inclusion of pericycle in the definition is unfortunate because of the present-day controversy over the true nature of the pericycle. However, eustele seems to be the most appropriate term and will be used in this article.

Recent work has brought out the fact that dicotyledonous steles are composed of the lower extensions of leaf-traces and, except in certain aquatics, are not made up of cauline bundles but of foliar ones. Thus, there is no procambial nor vascular tissue above the last-formed leaf, and there is an increase in the number of bundles of the stele progressively down the stem as the number of leaves attached to the stem increases. If viewed in three dimensions, the *primary* vascular system is a series of leaf-traces, the lower extensions of which form a eustele whose bundles are arranged cylindrically. Within this stele anastomoses of bundles occur in various ways depending upon the species of plant. It is questionable, therefore, whether foliar gaps, comparable to those found in siphonostelic ferns, are recognizably present in a *primary* vascular cylinder of the eustelic type. In any case, the parenchymatous interfascicular parts of such a stele are so diverse and extensive that the limits of hypothetical foliar gaps are not detectable. Clearly definable gaplike structures appear only after the formation of secondary tissue and are then parenchymatous lacunae in the *secondary* body. Since the flower is a shoot whose primary vascular stele is formed by strands

of the appendages in basically the same manner as in a vegetative apex, and since the association of the traces with the interfascicular regions may be very complex, the term gap will not be used. The parenchymatous regions between the bundles will be referred to as *interfascicular regions*.

Leaf-trace has been used as a collective term for all strands "entering" a leaf (European and older workers), and also for each strand to a leaf, or each strand or strands from a single "gap" (American and more recent workers). For reasons which will become apparent in the text, the concept of a single strand as a trace will be followed here, the trace being that part of the strand between the base of the appendage and its point of departure from the stele or from a cortical bundle (see below). Thus, strands which divide in the cortex will be considered *double traces*, whereas stelar bundles which divide and give rise to two or more strands within the stele and then exit as separate strands will be considered as separate traces. Furthermore, bundles which "leave" the stele and later divide in the cortex into two or more traces that "enter" *different* appendages will be called *cortical bundles*.

INFLORESCENCES

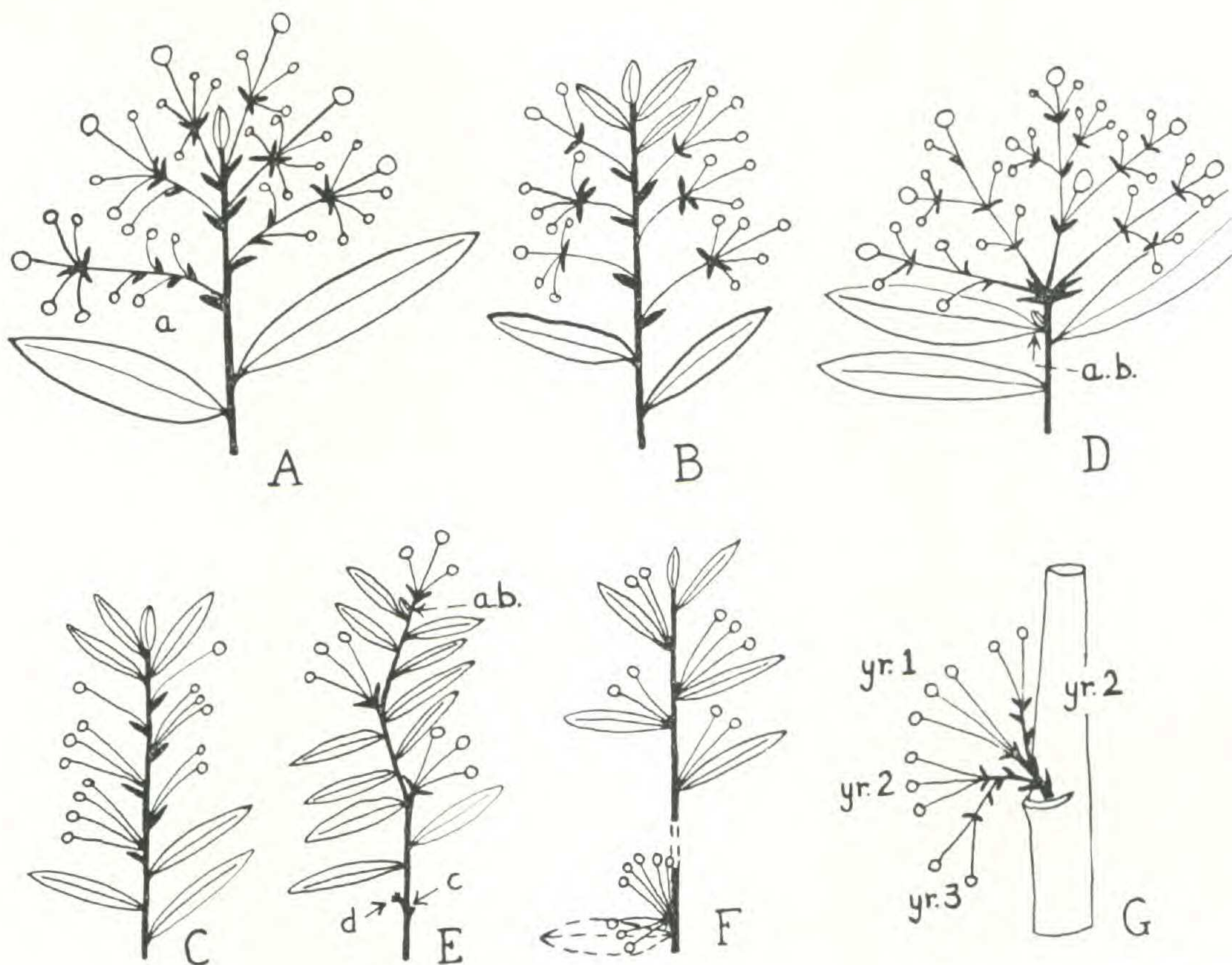
According to Parkin's (10) terminology, the inflorescences of the Winteraceae are either intercalary or pseudoterminal. The latter type gives rise to a sympodial branching system, whereas the intercalary type produces a monopodial branching system. The inflorescences of *Drimys* are intercalary, that is, the inflorescences are borne in axils of bracts (or occasionally leaves) below the terminal bud, which later produces leaves and inflorescences in alternate periods of growth. The flowers of *Drimys* Section *Wintera* are variable in number in each of the cyme-like inflorescences and are usually pedunculate. The whole group of axillary inflorescences may give the appearance of an umbel-like structure, especially before the terminal bud has developed into foliage (*text-fig. A*). In *D. granadensis* var. *grandiflora* Hieron. (*text-fig. A*) each inflorescence consists of an apical flower, below which is a whorl of a variable number of flowers subtended by bracts. The number of these bracts does not necessarily correspond to the number of flowers they subtend. Below this whorl there may or may not occur one to four spirally arranged flowers (*a*), each subtended by a bract. An examination of the American species of *Drimys* reveals that a reduction from this rather complex type of inflorescence evidently has occurred in this group until only two or three flowers remain in the inflorescence (*D. brasiliensis* var. *campestris* (St. Hil.) Miers) (*text-fig. B*).

In the Section *Tasmannia* of *Drimys* the flowers are borne singly or in fascicles of two to four flowers (usually three). A bract (occasionally a leaf, e. g. *D. Brassii*) subtends each flower or fascicle. These flowers are without peduncles (*text-fig. C*).

The inflorescence of *Bubbia* consists of cyme-like pedunculate flower-groups developing in axils of bracts at the terminus of a branch (*text-fig. D*). The branch continues its growth from a bud in the axil of a leaf

immediately below the inflorescence (*a.b.*). It is the pseudoterminal inflorescence as defined by Parkin, who cites species of "*Drimys*" (really species of *Bubbia* and *Belliolum*) as examples. The pseudoterminal inflorescence, according to Parkin, has developed from an intercalary type by the abortion of the terminal bud. In other words, a group of axillary inflorescences are congested at the apex of a stem and the structure as a whole appears to be terminal because the apical bud is absent. The number of flowers in the inflorescences of *Bubbia* varies considerably; thus, there is formed a series of inflorescences from very complex, much branched types to fairly simple types with only a slight amount of branching. Occasionally an inflorescence is borne in the axil of a leaf (e. g. in *B. longifolia* A. C. Sm.) below the pseudoterminal flower-cluster.

Belliolum has pseudoterminal inflorescences very similar to those of *Bubbia* and also with great variation in the complexity of the flower-cluster. However, many species have inflorescences reduced to three non-pedunculate flowers (*text-fig. E*) and with only two bracts present. The inflorescence-bearing shoot persists after the development of the vegetative bud and usually appears to be lateral on older branches (*d*).



FIGS. A-G. Diagrams of inflorescences. A. *Drimys granadensis* var. *grandiflora* Hieron.; B. *D. brasiliensis* var. *campestris* (St. Hil.) Miers; C. *Drimys* Section *Tasmania*; D. *Bubbia*; E. *Belliolum Kajewskii* A. C. Sm.; F. *Pseudowintera*; G. *Pseudowintera*: short shoot drawn with elongated internodes to show nature of branching. *a.* spiral flowers; *a. b.* axillary buds; *c.* leaf scar; *d.* inflorescence scar; *yr. 1, 2, 3.* seasonal growth of short shoot.

The inflorescences of *Exospermum* and certain species of *Zygogynum* are essentially similar to the more reduced forms found in *Belliolum*. In other species of *Zygogynum* (*Z. Vieillardii*, *Z. Bailloni*, *Z. bicolor*) the flowers are solitary and terminal. If Parkin is correct in assuming that the pseudoterminal inflorescences of *Bubbia* and *Belliolum* were derived by the loss of the terminal buds from the intercalary inflorescences of *Drimys*, then the solitary terminal flower of *Zygogynum* must be an evolved form. It could not be a primitive terminal flower as Parkin contends. Growth of the axis is continued by an axillary bud basal to the terminal flower.

In *Pseudowintera* the main axis of the branch bears a terminal foliage bud. The flowers are often described as axillary and fasciculate. However, they are actually borne terminally on extremely compressed short shoots which bear several very small reduced bracts (*text-fig. F*). These short shoots are capable of bearing flowers each year for several seasons. Buds in the axils of the bracts produce in the second year of growth other compressed shoots with flowers and bracts. These secondary shoots in turn produce buds in the axils of their bracts, buds which develop the third seasonal growth of flowers. If this short shoot were elongated as drawn in *text-figure G*, it is apparent that the structure is a branching system so reduced that only flowers and bracts are formed. Each segment of this system is comparable to the reduced pseudoterminal inflorescences of *Belliolum*, *Exospermum*, and *Zygogynum*. However, a foliage shoot may develop from a bud in the axil of a bract in the second growth season instead of a reduced flower-shoot.

PEDICELS

The peduncles, i. e. primary, secondary, or tertiary rays of the inflorescences, usually have well-developed eusteles of a variable number of bundles. This is especially true of *Drimys*. The bracts subtending the inflorescences of *Drimys* have three traces with distinct lacunae in the secondary body (*fig. 1*) except for occasional bracts with two traces. The bracteoles subtending the pedicels of the flowers in *Drimys* also have three traces in most specimens examined, although bracteoles with one trace are fairly prevalent. In *Bubbia*, however, all bracteoles examined have one trace (*fig. 2, A and B*), each trace being extremely minute even in large flowers of *Bubbia Clemensiae* A. C. Sm. These traces in *Bubbia* arise at a higher level than the bracteoles, necessitating a downward bending of the trace for a short distance (*fig. 2, B and A*). In laterally borne fasciculate flowers (*fig. 1*) the vascular cylinder of the branch is greater in diameter at those regions where flowers arise. A single bract subtends each flower (*ped.* in *fig. 1, C and D*) or each floral cluster. Extra bracts may be present (*fig. 1, A and B*). Each thickened area of the stele breaks up into a number of bundles as it leaves the central cylinder and almost immediately assembles into steles of the floral pedicels (flower cluster 3, *fig. 1, F-I*). These pedicels may contain one or two concentric bundles (*fl. cl. 2, fig. 1, H*) or a cylinder of bundles. The number of bundles present in the base of the pedicel varies greatly.

The formation of pedicels from the rays of the inflorescences and the formation of primary, secondary, and tertiary rays in a flower are similar in both *Drimys* and *Bubbia*. The number of bracteoles for each group of flowers varies from two to five in *Drimys* and is constantly two in *Bubbia*. The number of flowers in the cluster, however, is not indicative of the number of bracteoles. The vascular cylinder of the ray or peduncle separates into the steles of the floral pedicels as depicted in *figure 2*. One flower of the cluster is terminal. The number of bundles entering each pedicel varies from two large bundles to well-dissected eusteles (*figs. 3 and 5*). Distinct cylinders are always present in the pedicels of *Belliolum*, and almost always in *Drimys* Section *Wintera*. In *Drimys* Section *Tasmannia* and in *Pseudowintera* the number of bundles is less. Often there are only one, two, or four. Two wide interfascicular regions, one above the bracteolar trace, the other above the attachment of the bundles to the peduncular cylinder, are often retained for long distances in the pedicel (*lg. rays, figs. 4 and 5*). In flattened pedicels these interfascicular regions are located in the flattened sides of the cylinder and the vascular bundles are grouped in the two narrow arcs of the cylinder (*figs. 3 and 4*). However, all large interfascicular regions are not always identical to these interfascicular regions. The bundles of the stele (*fig. 7*) branch and anastomose throughout the length of the pedicel, thus producing new interfascicular regions and eliminating some of the lower ones (*fig. 6*). Accessory interfascicular regions¹ (*acc. r., fig. 7*) are also produced, interfascicular regions which are not related to any external appendage of the pedicel and which are due to a splitting of the bundle. If the interfascicular regions of the pedicel (*fig. 7*) are followed upward into the torus (*fig. 9*), it will be seen that most of them are closed at some level in the torus. Furthermore, many of the interfascicular regions, as well as the accessory ones, extend several internodes and have no relationship to appendages even in the torus. Interfascicular regions of this nature are most prevalent in *Drimys* but occur also to a lesser degree in flowers of the other genera (*acc. r., fig. 12*). Thus the vascular system of the pedicel and the torus should be considered as a network of branching, rebranching, and anastomosing strands rather than as a stereotyped cylinder dissected by the exit of traces to appendages. This interpretation is substantiated by the examination of cleared flowers where the entire vascular system is seen as a unit. It will be made clearer when the torus is examined in detail.

CALYX

Bubbia and *Drimys* are separated taxonomically by their calyces. *Drimys* has a calyptrate calyx with two lobes, rarely three. In *Bubbia* the calyx does not enclose the flower-bud and the number of lobes is more variable (2-9, usually 3). *Belliolum* has an entire or an inconspicuously

¹Also known as perforations (F. O. Bower. *The Ferns*. Vol. I. 1923; O. Posthumus. *On some principles of stelar morphology*. Amsterdam. 1924. Trans.). However, the term perforation gives a connotation of a hole, to which the author objects.

lobed calyx, while *Pseudowintera* has an entire, crenulate, or bilobed calyx (Smith 11, 12, 13). The calycine traces of the Winteraceae are predominantly branches of bundles and not whole bundles of the central vascular cylinder. The traces usually arise from the sides of the stelar bundles, occasionally from the center. More than one trace may be adjacent to the same interfascicular region (center of *fig. 9*), which is widened when the traces "depart."

The number of traces to the calyptrate calyx of *Drimys* varies from five to eleven. Since three traces are found in the leaves, bracts, and most bracteoles, three traces can be considered the basic number for each part of the calyptra. If this is true, then three-fifths of the calyces of *Drimys* examined would be two-parted or bilobed, and two-fifths would be three-parted or three-lobed. This raises a question regarding Dr. Smith's statement (12:6) that the sepals of *Drimys* Section *Wintera* are usually two, rarely three in number. However, in buds where the two free tips of the sepals were unbroken, it was found that one sepal received a greater number of traces, four traces in a seven-trace calyptra, often five in an eight-trace calyptra, and six in a ten-trace calyptra. This condition may be interpreted in two ways: (1) the number of traces in the sepal whose tip overlaps the tip of the other sepal has been increased because of size difference of the sepals, or (2) this "outer" sepal is really a composite of two sepals which through phylogenetic changes has already lost externally all indications of its two-parted nature except in rare instances.

The number of traces in the calyx of *Bubbia* varies from three (often double traces) to twelve. Each lobe of the calyx receives, basically, three traces, so that in the specimens examined a calyx with two lobes has usually six traces, with three lobes nine traces, and with four lobes twelve traces. However, there may be fewer or more than the usual three traces to each lobe. For example, in *figure 12* one of the two calycine lobes has one trace which is a double trace, and the other lobe has one double and one single trace.

In *Pseudowintera axillaris* (J. R. & G. Forst.) Dandy, all specimens examined have two traces which arise on opposite sides of the toral stele. Although externally the calyces of the two varieties, *P. axillaris* var. *colorata* (Raoul) A. C. Sm. and *P. axillaris* var. *typica* A. C. Sm. (13), appear different, the vascular anatomy suggests for both a two-parted calyx, each part with one trace. The reduction of trace-number may be correlated with the reduced size of the flower in this genus.

The toral vascular system of *Belliolum* is much more complex than those of the other three genera. Here cortical bundles arise from the stele and divide in the cortex to form traces which enter appendages borne on different levels of the torus. This complex type of toral system is very similar to the condition found in *Himantandra* (1). In *B. haplopus* (Burt) A. C. Sm. there are nine cortical bundles, each of which usually divides into three parts. The central branch is a calycine trace. The lateral branches unite with laterals from the adjacent cortical bundles to form petaline

traces. But in *B. Burttianum* A. C. Sm. the calycine traces arise directly from the stele and branch, anastomose, and rebranch at the base of the calyx. However, cortical bundles are formed in the region of the petals. In *B. Burttianum* there are seven to nine calycine traces, which are assembled into two groups on opposite sides of the toral cylinder. As this species has an inconspicuous bilobed calyx, in contrast to the essentially entire calyx of *B. haplopus*, the position and not the number of the traces seems to indicate the apparent number of sepals. The number of traces would indicate either two or three sepals. *Belliolum haplopus*, with nine uniformly spaced traces, can be considered as having three sepals.

PETALS

The number of petals in the Winteraceae varies from two (rarely one or none) to many. The number of principal veins per petal is usually three or five, and the number of traces either one or three. Occasionally the inner small petals of a flower may have one or two traces instead of the usual three. All petals of the examined specimens of *Drimys* Section *Wintera* and most petals of those of *Drimys* Section *Tasmannia* have one trace. An interesting condition occurs in *D. obovata* A. C. Sm., where the two traces, one to each of the two petals, arise from cortical bundles from which calycine traces also are formed. The petals of *Belliolum* and *Pseudowintera* always have three traces, except for occasional one-trace inner small petals of *Belliolum*. As stated previously, *Belliolum* is distinct from the other genera because of the more complex branching system. In *B. haplopus* the lateral branches of the cortical bundles, which also formed the calycine traces, become lateral traces to the lower petals. In both species of *Belliolum* examined, cortical bundles arise in the petaline region and divide once or twice. One of the branches is always a medium petaline trace, the other (or others) may either immediately become a lateral trace for the next or higher petal or may remain as a cortical bundle which forms lateral traces to the succeeding series of petals. The median trace of the most apical petals usually arises directly from the stele, but occasionally it arises from a cortical bundle which also forms a trace to a stamen. In *B. haplopus* there are about four cortical bundles which remain as cortical bundles up to the base of the carpels, where they stop, never entering any appendage. These cortical bundles may be either those that arose in the calycine or in the petaline regions.

The petaline traces, like the traces of the calyx, are branches of the toral bundles (figs. 9 and 12). Occasionally a trace may be double (fig. 12, trace 1) or a stelar bundle may divide in the stele to form two traces to the same petal (fig. 12, trace at 2) or to different petals (traces 3 and 4). Other complications may arise, such as two small toral bundles uniting in the stele to form one trace (traces 5 and 6). In flowers with three-trace petals, all of the traces may be adjacent to the same interfascicular region or to different interfascicular regions. Furthermore, the traces to one petal may even arise from the same large stelar bundle when the vascular cylinder is composed of a small number of bundles, as in the diagram of figure 12.

In flowers with one-trace petals and with many bundles in the toral stele, this congestion of traces does not occur (*fig. 9*). Here, more than one petaline trace is rarely adjacent to the same interfascicular region, although staminal and petaline traces may be adjacent to the same one.

STAMENS

Without exception the stamens in all genera of the family receive one trace. In many places several staminal traces arise from the same interfascicular region, or even from the same one as a petal (*figs. 9* and *12*).

Where many spiral appendages are so congested, as in winteraceous flowers, congestion of the traces will necessarily occur. Also, with more traces to the appendages, the more complex the relation of those traces to the stele becomes. This was shown in the description of the petaline traces of *Bubbia* (*fig. 12*) and also in *Belliolum*. It is also evident in the staminal region, e. g. in *Drimys*, where several traces arise from the same toral bundle and are related to the same interfascicular region. The floral vascular structure, therefore, is really a network of branching and anastomosing stelar strands from which appendicular traces arise in no definite pattern. Because of the shortened internodes and closely-compressed floral appendages, these traces seem to unite to the nearest strands, so that a series of traces may be associated with the same interfascicular region which may extend not only for a couple of nodes but throughout the length of the flower.

CARPELS

The carpels are inconstant in number in the winteraceous genera. In the species studied the variation ranged from one to thirteen. All residual vascular bundles of the central cylinder above the lower appendages enter the carpels (*figs. 8, 9, 11, and 12*). No "superfluous" tissue remains above the carpellary traces, as Eames (5) figures in *Prunus*, *Actaea*, and *Bauhinia*. The floral apex, which is quite prominent in some species of *Drimys* (*fig. 8, G*, and also *fig. 6* in reference 3), is, therefore, non-vascularized. In *Drimys* and *Bubbia* there are usually only a few fairly large strands remaining after the stamen-traces have made their exit (*figs. 8, E* and *11, C, D*). Often the appearance of a vascular ring in transverse section is lost. In *Pseudowintera* and *Belliolum* a definite ring consisting of many bundles is present. An anastomosing of bundles occurs below the carpels so that the number of bundles is reduced to a greater or less extent. Concentric bundles (*fig. 8, F*), the number corresponding to the number of carpels in the flower, are formed predominantly in *Drimys* Section *Wintera*. Crescent-shaped bundles, one to each carpel (*fig. 10*), are also quite prevalent. These bundles are located in the torus (*fig. 8, E* and *F*) and in the lower part of the carpellary stipe. Each divides into three collateral bundles (two ventrals and one dorsal trace) slightly below the ovarian cavity, or at the base of the carpellary stipe (*fig. 8, F*). In a few instances two or the usual three traces enter the carpel directly from the toral cylinder without a preliminary union into one large bundle. If two bundles enter the carpel, one eventually divides into the two ventral bundles. All these variations

may occur in the same flower. In *Drimys* Section *Tasmannia* one bundle, either concentric or collateral, enters each carpel in the majority of specimens examined. However, there are more cases (a third of the carpels cut) of two- and three-trace carpels than in Section *Wintera*. A few carpels have four or more traces. The long carpellary stipe of *D. stipitata* Vickery usually has one bundle, sometimes two, in the lower half and always two in the upper part. Since uni-carpellate flowers may have any of these vascular patterns, there is no correlation between the number of carpels in the flower and the type of vascular system present. In *Bubbia* the reorganization of the toral bundles into concentric bundles occurs only occasionally. Two and three traces are quite prevalent (figs. 11 and 12). The dorsal traces leave the toral system first when three traces enter the carpel. The ventrals are formed by the branching of the few remaining toral bundles. Many of the carpels have four and five traces. Often in a five-trace carpel the two extra strands are two lateral bundles situated between the ventral and dorsal bundles, one on each side of the carpel. However, when more than three traces are present there may be branching, anastomosing, and reassembling of the bundles in the torus or in the base of the carpel. In those carpels with extra large dorsals, as in *B. megacarpa* A. C. Sm., *B. longifolia* A. C. Sm., and *B. monocarpa* A. C. Sm. (see illustrations in reference 3), a number of bundles may unite in the toral cylinder to form the dorsal trace. In the branching, anastomosing, and reassembling of the toral bundles into carpellary traces, bundles from one side of the torus may cross over and unite with strands on the opposite side (figs. 11, C and 12).

In *Pseudowintera* the number of carpellary traces is usually three, often four, and rarely one or five. Although a definite cylinder is left in the torus after the stamen-traces depart, the cylinder is made up of relatively few bundles. In *Belliolum*, however, this residual cylinder is made up of a greater number of bundles (8-16). The dorsal traces in *B. haplopus* depart from the cylinder first and the remaining bundles divide, when fewer toral bundles than ventral traces are present, or anastomose, when a greater number of toral bundles are present, to form the two ventrals. In *B. Burtianum*, which has one carpel in the flower, several bundles unite in the cylinder to form the dorsal strand. This may occur before all of the stamen-traces have departed. The rest of the toral bundles unite into four or five traces which are ventrals and laterals.

DISCUSSION

The floral vascular system of the Winteraceae should be considered as a network of branching and anastomosing strands, with little uniformity in pattern. It is a vascular system which is appendicular rather than cauline, that is, all the bundles of the stele are downward extensions of the appendicular traces or the composite of these extensions. There are no cauline bundles which extend from the pedicel through the torus and end blindly at the apex of the vascular cylinder. The vascularization of these flowers is very similar to that found in foliar stem-tips where leaf-traces form the

stele. Just as in the foliage-tip, there is no vascular tissue developed above the last-formed appendages in the flower. The vascular system differs from that of the foliage-tip in the haphazard manner of the insertion of the traces in the stele and the irregular association of the traces to interfascicular regions. Interfascicular regions may extend from the apex of the torus to the base of the pedicel (*fig. 9*, interfascicular region between third and fourth carpel bundles), or they may be very short. The number of traces associated with an interfascicular region varies greatly, as does the manner in which the traces or their extensions unite within the stele with extensions of the more apical traces. Furthermore, the traces from different appendages may be associated with the same interfascicular regions. These irregularities are due to the large number of appendages crowded within a small area. In a stem-apex where the internodes are longer, the union of trace-extensions within the stele seems to be of a definite pattern² and the interfascicular regions are, therefore, of fairly uniform length and distribution. This vascular instability of the flower may be reflecting the phylogenetic changes that are still occurring in this rather primitive group of plants.

The variation in the number of calycine lobes and in the number of traces to the calyx of the Winteraceae indicates that changes have occurred and are occurring in this region. There is evidence that the apparently two-parted calyptrate calyx of *Drimys* actually consists, or formerly consisted, of three sepals. In both *Drimys* and *Bubbia* three traces to each sepal are predominantly found. However, in the two-lobed calyces of *Bubbia* there is a tendency toward a reduction in the number of traces (*fig. 12*). The culmination of reduction occurs in *Pseudowintera*, where one trace enters each of the two sepals. The number of traces to the petals and to the stamens shows nothing unusual, although their mode of insertion in the stele illustrates again the instability of a changing toral vascular system.

The occurrence of concentric and crescent-shaped bundles in the carpellary system is especially interesting. These bundles are remarkably like the bundles often found in petioles and suggest that a petiole-like structure may have occurred in the lower region of the primitive carpel. Not in all cases are these bundles in the stipe itself, but their occurrence in the torus may mean their gradual loss concomitant with the loss of an external petiole-like region. Their prevalence in *Drimys*, where the carpels are the most primitive of the Winteraceae, is significant. However, their more frequent occurrence in the Section *Wintera* is unexplainable, since *Drimys* Section *Tasmannia* has the more primitive carpels of the genus (3). In the other three genera, where modifications of the *Drimys* Section *Tasmannia* carpel occurs (3), the "normal" three-trace condition (or variations of it) is predominant and the petiole-like vascular region is absent.

²Katherine Esau. Vascular differentiation in the vegetative shoot of *Linum*. II. The first phloem and xylem. *Amer. Jour. Bot.* 30: 248-254. 1943. Note diagrams in *text-figures 1 and 9*.

Carpels with two traces, one trace for the dorsal and one trace for the two ventrals, may be weakly retaining the petiole-like vascular condition which occurs in *Drimys*.

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EXPLANATION OF PLATES

PLATE I

FIG. 1, A-I. *Drimys piperita* Hook. f., *Griswold 44*. Serial segments of the vascular tissue in a flowering shoot with lateral flower clusters. Stele is drawn as solid cylinder because secondary tissue is present. Approx. $\times 15$. FIG. 2, A-E. *Bubbia semecarpoides* (F. v. Muell.) Burt, *White*. Serial segments of peduncle with bases of the three terminal floral pedicels. Approx. $\times 12$. Bud scale of terminal bud, *b. sc.*; bract, *br.*; flower cluster 1, 2, 3, *fl. cl. 1, 2 and 3*; pedicel, *ped.*; terminal bud, *t. b.*

PLATE II

FIG. 3. *Drimys piperita* Hook. f., *Ramos 19583*. Transverse section from base of pedicel. Approx. $\times 35$. FIG. 4. *Drimys Brassii* A. C. Sm., *Brass 9536*. Transverse section from base of pedicel. Approx. $\times 42$. FIG. 5. *Drimys insipida* (R. Br.) Pilger, *White 3568*. Transverse section of pedicel slightly below torus. Large rays, *lg. r.* Approx. $\times 42$. FIG. 6, A-D. *Drimys brasiliensis* var. *campestris* (St. Hil.) Miers, *Clausen, F. M. 1024472*. Cross-sections of pedicel at levels designated *a-d* in figure 7. Arrows indicate position of bundles from left to right in diagram of figure 7. Approx. $\times 45$. FIG. 7. Same as fig. 6. Diagram of vascular system in pedicel showing branching and anastomosing of strands. Lightly stippled regions mark part of system omitted. Levels drawn in figure 6 indicated by *a-d*. Accessory ray, *acc. r.*

PLATE III

FIG. 8, A-G. Same as fig. 6. Cross-sections of flower at levels designated *a-g* in figure 9. A, base of torus; B, level of calyx; C, level of petals; D, level of stamens; E-G, levels in apex of torus and base of carpels. Arrows indicate position of bundles from left to right in diagram of figure 9. Sterile apex, *st. ap.* Approx. $\times 20$. FIG. 9. Same as fig. 6. Diagram of vascular system in flower. Heavy broken lines represent branching of calycine traces. Petaline traces not marked. Apical strands are traces to the five carpels.

PLATE IV

FIG. 10. *Drimys Winteri* var. *chilensis* (DC.) A. Gray, *Junge*. Cross-section of torus above stamens, showing types of bundles which will enter the seven carpels. Approx. $\times 30$. FIG. 11, A-E. *Bubbia Whiteana* A. C. Sm., *Kajewski 1495*. Cross-sections of flower at levels designated *a-e* in figure 12. Arrows indicate position of bundles from left to right in diagram of figure 12. Dorsal veins, *dor.*; ventral veins, *ven.* Approx. $\times 42$. FIG. 12. Same as fig. 11. Diagram of vascular system in flower. Lightly stippled regions mark part of system omitted. Accessory ray, *acc. r.*

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